AN ICHTHYOSAURIAN SKULL FROM QUEENSLAND.

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(Plates XV and XVI and Text-figures 1 and 2.)

The remains which are the subject of this paper were found at Galah Creek, about twelve miles from Hughenden, in the Rolling Downs formation (Lower Cretaceous) of Western Queensland, and were collected, forwarded, and kindly donated to the Queensland Museum by Mr. S. Dunn and Mr. William Elliott in May, 1914. It is my pleasant duty heartily to thank these gentlemen for their enthusiastic work in securing this large and valuable specimen for our collections.

Material.—As will be seen from the profile view, illustrated in Plate XV., this large skull is in six pieces. The extreme end of the rostrum is missing, but, judging from the structure of the anterior part preserved, only a small portion would be needed to complete the skull. Gilmore[1] has pointed out how frequently the extreme anterior segment is missing in Ichthyosaurs, and how fractures are caused by the cracking of specimens when enclosed in an elongate concretionary mass.

The skull is massive, with a maximum length (mandibular) of 1,026 mm., and a maximum width (articular area of mandible) of 395 mm. It is evident that great changes have taken place since it came to rest. As a result of tremendous vertical pressure, the whole of the teeth, with the exception of broken roots, have been forced from the continuous dental grooves, characteristic of *Ichthyosaurus*, and the premaxillary and mandibular rami are now in juxtaposition. Fortunately, many of the teeth have been preserved, mostly as fragments, on the lateral and lower surfaces of the jaw. In the posterior part of the skull there are still greater evidences of changes under intense pressure. On the left-hand side the orbit has been crushed down and its original contours are not distinguishable. As a result of this lateral torsion, the mandible has been somewhat displaced to the right. The supratemporal fossæ are preserved in fairly symmetrical condition. Great difficulty has been experienced in studying some of the component parts. The distortion of the skull is accompanied by a very close investiture of the remains by a fine hard limestone matrix, which in places is almost indistinguishable from the actual fossil. The matrix involving *Cratochelone berneyi*,[2] described by the author in 1915 from the same district, was very similar in texture. This investing material evidently penetrated the skull after the decay of cartilage, cementing the disrupted elements together.

[1] C. W. Gilmore, Mem. Carnegie Mus., Pitts., II, 1905, p. 80.

[2] H. A. Longman, Mem. Qld. Mus., III, 1915, p. 25.

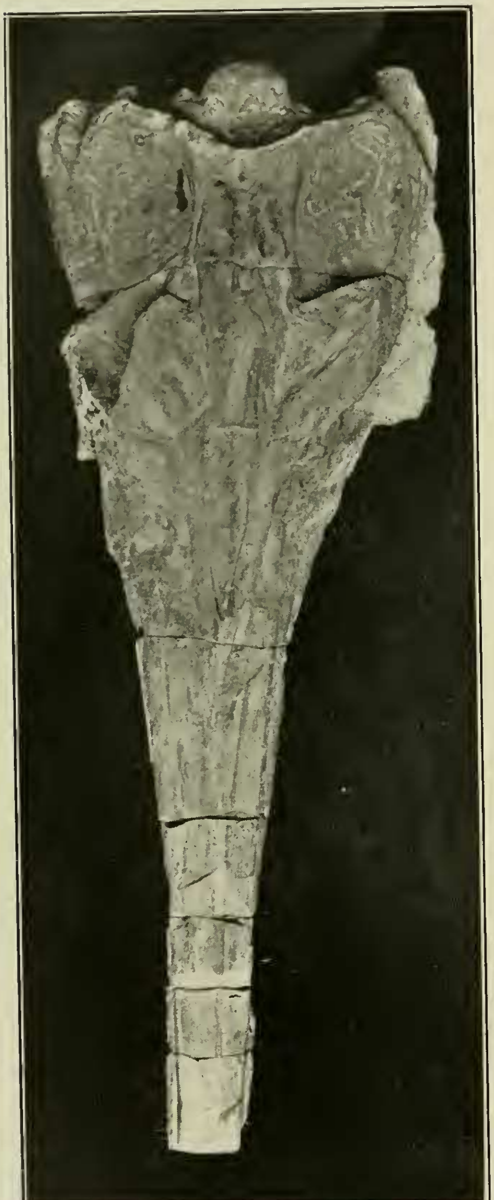

Fig. 1.—Skull of Ichthyosaurus australis. Superior view.

Fig. 2.—Skull of Ichthyosaurus australis. Lateral view. Approximately one-seventh natural size.

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On the upper part of the skull the elongate premaxillæ can be traced back for a distance of 615 mm. to the narial openings. Between these two bones in the superior surface is a well-marked symphysial groove. The nasals are exposed from beneath the premaxillæ at about the anterior third of the length of the skull, and at first are on a lower plane than the hemispherical superior borders of the diverging premaxillæ, forming a triangular recess. Further back there is a secondary triangular depression, the borders of which are parallel to the anterior recess, but this is entirely internasal. Lateral divisions of the nasals extend outwards beyond the frontals towards the superior border of the orbits. Sutures with post frontals cannot be traced.

The external narial openings can be seen on both sides, but they are distorted. A semicircular raised border is present behind the openings. Incomplete maxillæ are present, but the sutures between them and the lachrymal bones and the jugals cannot be positively traced on either side.

In the region of the frontals a remarkable rectangular raised process was present in the undisturbed fossil. On careful development this proved to be mainly matrix closely investing a troughlike depression, with raised lateral borders, as may be seen in Plate XV. At first this was thought to be a veritable raised bony border surrounding the pineal foramen, and suggesting an unusual development of "the third eye," but the true foramen is apparently situated in a more posterior position. This closely adpressed structure consists of two parallel bars, thinly joined anteriorly; the bars are 90 mm. in length and are symmetrically disposed at a distance of 10 mm. from the median line. If this structure is actually *in situ*, which seems unlikely, it would demand generic recognition. The frontal bones evidently do not extend far beyond the area of this structure. In view of the partial disorganization of the specimen, possibly associated with an attack from other predaceous or scavenging monsters of the period, it is suggested that this curious structure represents an inverted cranial element. It cannot, however, be allocated with any of the bones, the contours of which are so clearly demonstrated by Sollas' classic sections,[3] and possibly represents hyobranchial elements. And it is, of course, possible that further material will demonstrate characters which will warrant the establishment of a new genus for this large Australian Ichthyosaur. The prominent ridges, which are present in the parietal region and on the nasal bones, appear to be distinctive features. From the occipital border of the parietal region a convex median ridge extends anteriorly, and this is accentuated by the presence on each side of elongate valleys, the lateral sides of which curve upwards to form the borders of the supratemporal fossæ. At the anterior termination of the median ridge there is a cavity which could not be traced into the internal tables of the skull, but which probably represents a disrupted pineal foramen. This is nearly in line with the anterior borders of the supratemporal fossæ, and is thus in the usual position for the foramen.

[3] W. J. Sollas, Phil. Trans. Roy. Soc., B, 208, 1916, pp. 66-126.

In the temporal region the anterior horn of the squamosal extends to the middle of the large oval fossæ, articulating with the postorbital. The fossæ are fairly symmetrical, approximately 120 mm. in length, with a breadth of 75 mm.

On the right-hand side the orbit is well preserved, except for its posterior border. The cavity has been largely set free from the cement-like matrix, which here contained molluscan fragments. It was carefully excavated in the hope that the characteristic sclerotic plates, possibly driven inwards, might be exposed, but these have entirely disappeared. It is evident that the orbit was the characteristic oval. Its vertical diameter at the periphery is 110 mm. Beneath the orbit, portions of the jugal can be seen, but the full extent of the zygomatic arch with its sutures cannot be outlined. The jugal appears first as a raised process near the midline of the anterior border of the orbit and then curves down to form its lower edge.

A large supratemporal bone is present on the left-hand side, and its superior margin junctions with the lateral border of the squamoso-postorbital arcade. Much controversy has taken place over the "additional temporal bone," as S. W. Williston called it in the Ichthyosaurs, and the author has followed the nomenclature of Lydekker,[4] Sollas (*loc. cit.*), Gilmore, and Andrews in calling it supratemporal. Williston considered the inner bone of this "Diapsid" group the tabular and the outer the squamosal,[5] but in view of Watson's demonstrations[6] it is surely better to reserve the name "squamosal" for the more constant element. Perhaps the laterotemporal or "sclerodermal plate," as Owen called it, is really a separated division of the quadratojugal.

The quadratojugal is present, and its posterior portion is visible in the occipital region, where it forms the inferolateral border of the vacuity presented by the curved shaft of the quadrate. Its sutures with the supratemporal are obscure.

Basi-Occipital.—The stout symmetrically convex condyle extends backwards beyond the pterygoids for a distance of 33 mm.; the tranverse diameter is 74 mm., vertical diameter 64.

Basis Cranii.—The suture between the basioccipital and the basisphenoid can be traced, giving a length of 60 mm. to the former bone. The basisphenoid is about 75 mm. in length, and forms with the posterior element a rectangular rostrum for the support of the pterygoids. The basisphenoid has a visible width of about 60, whilst the basioccipital is about 40 mm. Near the posterior margin of the basisphenoid the opening of the single canal for the carotic arteries can be clearly seen; this foramen is circular and has a diameter of 10 mm. In the median line of the interpterygoid vacuities the splint-like parasphenoid may be seen, but this has been only partially freed from the matrix, compared with which it is very friable. This bone evidently increases in thickness towards its upper surface and is triangular in section. It can be traced anteriorly for a distance of 220 mm., where it is

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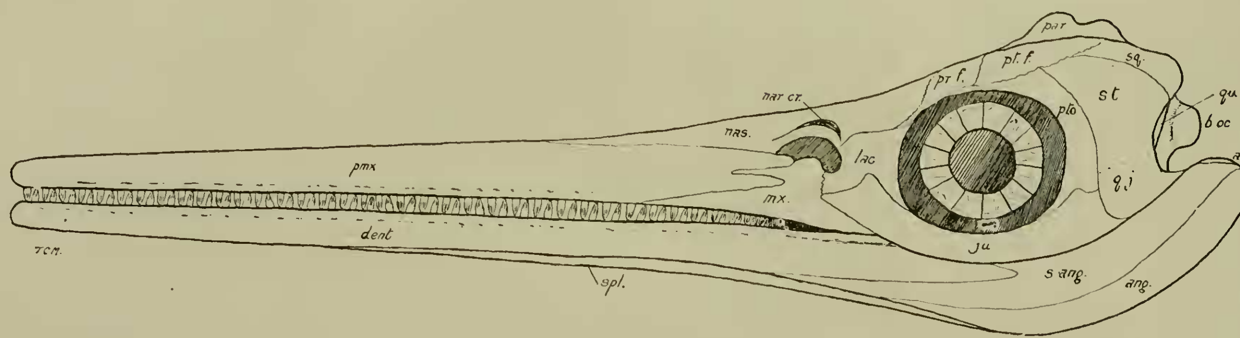
[4] R. Lydekker, Catal. Foss. Rept. Brit. Mus., Part II, 1889, p. 3.

[5] S. W. Williston, Phylogeny and Classification of Reptiles (Journ. Geo XXV), 1917, p. 416.

[6] D. M. S. Watson, Ann. Mag. Nat. Hist. (8) XIV, 1914, pp. 84-95.



Text-figure 1.—Reconstruction of the skull of *Ichthyosaurus australis*. Approximately one-seventh natural size. *Ang.*, angular; *art.*, articular (showing post-articular surface); *b. oc.*, basioccipital; *dent.*, dentary; *ju.*, jugal; *lac.*, lachrymal; *mx.*, maxilla; *nar. cr.*, narial crest; *nas.*, nasal; *par.*, parietal; *pmx.*, premaxilla; *pr.f.* prefrontal; *pt.f.*, postfrontal; *pt.o.*, postorbital; *q.j.*, quadratojugal; *qu.*, quadrate; *s. ang.*, surangular; *sq.*, squamosal; *sp.*, splenial; *s.t.*, supratemporal.

lost in matrix. The pterygoids provide the greater part of the base of the posterior moiety of the skull. On the left-hand side the pterygoid is in juxtaposition with and somewhat overlaps, owing to displacement, the basioccipital and basisphenoid. The right pterygoid has been tilted below the plane of the flanges presented by the axial bones. From the basioccipital to the lateral border the pterygoid attains a maximum breadth of 110 mm.

Owing to the presence of superimposed hyoid rods, and a brecciated mass of broken teeth and matrix containing associated fossils, the central portion of the lower surface of the fossil is obscured. The extent of the interpterygoid vacuities cannot be gauged, but, judging from the converging inner margins of the bones, the contours in this area are similar to the skull of *Ichthyosaurus longifrons* as figured by Owen.[7] The palatine elements appear to be displaced and are not visible in the same plane.

Posterior Region.—The contours of the superior border of the occipital region, formed by the parietals and processes from the squamosals, are quite continuous, being convex in the median area and then sloping to lateral concavities. Viewed from above, the postero-external borders of the squamosal are seen to curve symmetrically backwards, and, although the occiput is somewhat disrupted, the contours are quite elegant. The inner process of the squamosal unites in an oblique suture with the lateral arm of the parietal near the median line of the supratemporal fossa.

A large quadrate is present on each side, but owing to mandibular pressure these bones have been forced somewhat out of position.

Above the region of the foramen magnum, only small fragments are visible in the matrix of elements which correspond to the superior occipitalia, which have apparently been forced inwards. Possibly these are paired extensions of the supraoccipital which form part of the lateral borders of the foramen magnum.

The opisthotics are in place on each side, and junction with the basioccipital, the "stapes," and the squamosal.

Suggestions for a Re-interpretation of the so-called Stapes—

Next to the quadrate, the largest bone in the occipital region is the element called "stapes" by Sollas and Andrews. This acts as a strong lateral buttress of the basioccipital, and lies above the posterior flange of the pterygoid. It has an expanded facet for junction with the basioccipital, with an adjoining superior surface for association with the opisthotic. Cope,[8] who was the first to name this bone, did so with diffidence, and figured it as distinctly separated from the basi-occipital, whereas modern authors rightly show it as a buttress supporting the rostrum of the condyle. Owen[9] named it the paroccipital, but apparently only

[7] Owen, Liassic Reptilia, Mon. Pal. Soc., 1881, Pl. XXV.

[8] Cope, Proc. Amer. Assn. Ad. Sc., 1871, p. 199, fig. 2.

[9] Owen, Mon. *loc. cit.*, p. 94.

dealt with two pairs of occipital elements below the supraoccipital. C. W. Andrews notes that this bone (stapes) "seems to have lost its auditory function,"[10] and it is obvious that this so-called stapes cannot be associated with the fenestra ovalis, as Cope supposed. The stapes is usually regarded as the homologue of the hyomandibulare of fishes, and a large stapes is recorded for the Cotylosauria. Case figures the stapes of Dimetrodon,[11] a bone which in this and allied Permian reptiles is regarded by Broom[12] as the tympanic. The writer is unable to find, however, a parallel in literature to the interpretation of this buttress bone of the Ichthyosaurs as a stapes.

The columella auris of modern reptiles, the proximal end of which is presumably homologous with the stapes, is always placed antero-laterally to the basioccipital, and is quite distinct in position from this buttress bone.

The writer suggests that these lower lateral elements in the occipital region, the so-called stapes, should be interpreted as inferior divisions of the exoccipitals. That the upper elements are true exoccipitals seems to be demonstrated by the position of the foramen for the post-auditory nerves, as clearly shown in Andrews's illustrations (*loc. cit.*), and also by their relations to the foramen magnum. The unusual extension of the intermediate lateral occipitalia, the opisthotics, to the basioccipital, to which they also act as buttress bones, has probably brought about a division of the exoccipitals into upper and lower portions.

These lower lateral elements may thus be interpretated as inferior divisions of the exoccipitals. This change in nomenclature, giving the exoccipitals a ventral extension, appears to be generally supported by the position of the occipital elements in the Permian Tetrapoda studied by von Huene[13] and by R. Broom[14], and in the Stegocephalia illustrated by C. Wiman.[15] It is in consonance with the general arrangement of the bones in modern reptiles, where the exoccipitals are usually the lower lateral elements in juxtaposition with the basioccipital, the opisthotics uniting with them antero-superiorly in adult life (distinct in Chelonians); these relationships of the two elements are shown by Parker's studies of the development of the skull in the snake and the lizard.[16] It is not at variance with Howes and Swinnerton's interpretation of the development of the skull of *Sphenodon*.[17] It agrees also with the positions given by Kingsley in his diagram of the schematic vertebrate skull.[18] Huxley wrote that but for its large size he would have regarded the adjoining bone, now generally accepted as the opisthotic, as the stapes.[19]

[10] C. W. Andrews, Marine Rept. Oxford Clay, Brit. Mus., 1910, p. 11.

[11] E. C. Case, Bull. Amer. Mus. Nat. Hist., XXVIII, 1910, p. 190.

[12] R. Broom, Bull. Amer. Mus. Nat. Hist., XXVIII, 1910, p. 223.

[13] von Huene, Bull. Amer. Mus. Nat. Hist., XXXII, 1913, pp. 315-386.

[14] R. Broom, Bull. Amer. Mus. Nat. Hist. XXXII, 1913, p. 563, etc.

[15] C. Wiman, Bull. Geol. Inst. Upsala, XIII, 1915, Pt. 1.

[16] W. K. Parker, Phil. Trans. Roy. Soc., Vols. 169 and 170, 1878-79.

[17] Howes and Swinnerton, Trans. Zool. Soc., XVI, 1901.

[18] Kingsley, Outlines Comp. Anat. Vert., 2nd edit., p. 74.

[19] Huxley, Anatomy of Vertebrated Animals, 1871, p. 211.

The opisthotic or paroccipital very rarely appears to meet the basioccipital below the exoccipitals in other reptiles, although the relations between these elements are variable. The writer has diffidence in using terms that are not accepted by leading authorities, but the occipital region of the Ichthyosaurs provides material for several interpretations, and the use of exoccipital for the lower element seems to solve the difficulty of a most anomalous "stapes."

In the modern cetaceans the stapes is frequently reduced to a small conical plug, and, judging from analogy, the auditory functions of the Ichthyosaurs would not have been greatly utilised. Possibly the real stapes is the "long slender process" demonstrated in Section 494 of the very fine series in Sollas' great work (*loc. cit.*).

The stapes is often missing in fossils. The elaborate studies by D. M. S. Watson of the position of the fenestra ovalis in Therapsids, *Seymouria*, etc. (P.Z.S., 1914, and 1919) have an important bearing here, but the posterior aspect of the occipitalia in our specimen presents no evidence on this point.

The massive architecture of the occipital region was evidently associated with the attachment of powerful nuchal muscles. Perhaps a specialist will one day work out details of the probable musculature of the Ichthyosaurs on similar lines to the recent studies by Gregory and Camp on *Cynognathus*.[20]

LOWER JAW.—On the left hand side the lower jaw is practically complete, except for the missing anterior segment and a small portion of the angulare. The dentary is very elongated and is no less than 875 mm. in maximum length. Parallel with the alveolar border, and situated about 20 mm. below it, is a groove which is shallow anteriorly, but then deepens, giving the characteristic conjoined gun-barrel effect of the Ichthyosaurian rostrum. The posterior process of the dentary, which overlaps the surangulare, runs back to below the mid-region of the supratemporal fossa. Here the semi-spherical contours (in section) of the upper rod, or gun-barrel-like process, sink into the same plane as the surangulare and angulare.

The left angulare is not quite complete at its posterior end, and here its outer contours have been disturbed. It is a longer and more massive bone than the surangulare, but just at the termination of the dentary the two posterior elements are of equal depth. In this region the arrangement of the bones is very similar to the outer view given by C. W. Andrews for *Ophthalmosaurus* in Text-fig. 20 (*loc. cit.*), except that the angulare is distinctly extended to form the posterior portion of the mandible. Strong depressor muscles were evidently attached here, working with short leverage in association with the powerful levators placed in front of the articulation. Sollas points out that the levator muscles originating in the temporal region, inserted on the lower jaw, acting as levers of the third order, were "admirably adapted for snapping; and the Ichthyosaurus, from all that we know of it, must have obtained its food by seizing fish 'upon the wing.'"

[20] Gregory and Camp, Bull. Amer. Mus. Nat. Hist. XXXVIII, 1918, pp. 447-563.

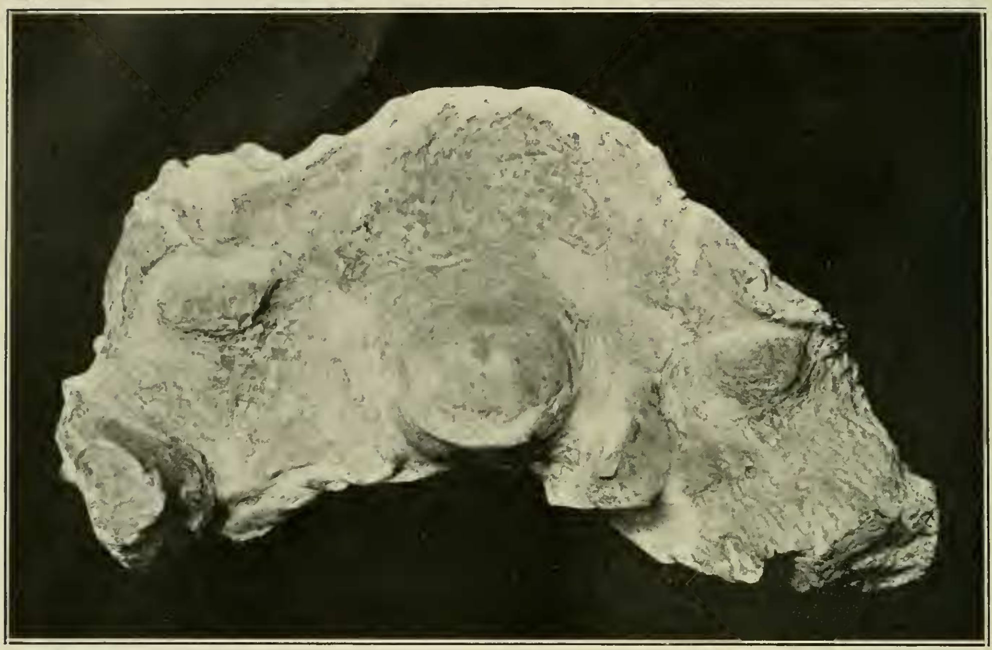


Fig. 1.—Skull of ICHTHYOSAURUS AUSTRALIS. Posterior view. Approximately one-third natural size.

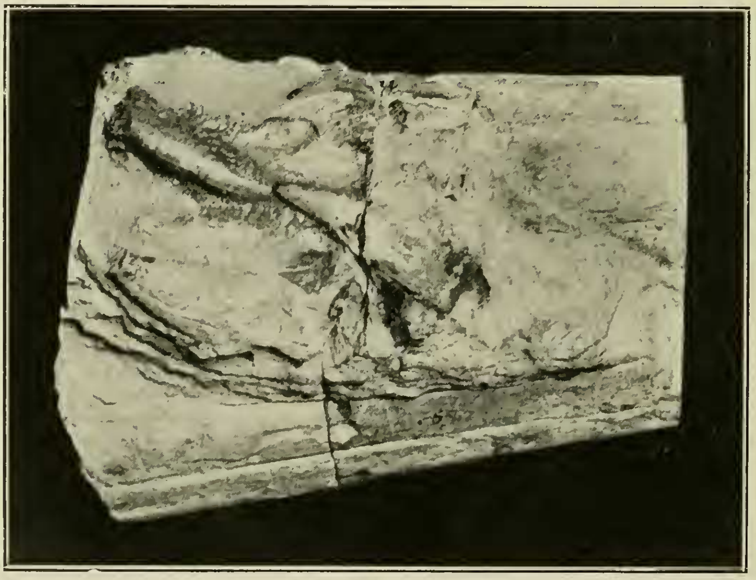


Fig. 2.—Anterior section of rostrum, ICHTHYOSAURUS AUSTRALIS, showing disrupted teeth. Approximately one-half natural size.

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